Does postcranial palaeoneurology provide insight on pterosaur behaviour and lifestyle? New data from the azhdarchoid *Vectidraco* and the ornithocheirids *Coloborhynchus* and *Anhanguera*

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ABSTRACT

The postcranial palaeoneurology of fossil reptiles is understudied, and those studies that exist focus predominantly on crocodyliforms and dinosaurs. The intervertebral foramina of the spine house nerves that exit to innervate surrounding tissues and the extremities. In the heavily fused (and typically distorted or poorly preserved) pterosaurian sacrum, intervertebral foramina can be difficult to observe and are rarely identified. The Lower Cretaceous azhdarchoid *Vectidraco* from the Isle of Wight, UK exhibits large, paired foramina on each sacral vertebra, originally identified as pneumatic foramina. Micro-computed tomography (μCT) imaging reveals these communicate with the neural canal and are intervertebral foramina for sacral nerves. The sacral vertebrae of *Vectidraco* are fused, and intervertebral foramina occur dorsolaterally on the centra. We identified these structures in other pterosaur sacra, including those of the ornithocheiroids *Anhanguera* and *Coloborhynchus*. The sizes of the sacral and notarial neural canals are compared and considered within interpretations of palaeoecology and locomotion, following previous studies. The relatively large sacral neural canal of *Vectidraco* implies a sacral enlargement for innervation of the legs and lumbosacral plexus. When compared with *Anhanguera,* this supports indications that azhdarchoids were more hindlimb-proficient than ornithocheiroids. Neural canal size in the *Coloborhynchus* notarium suggests that ornithocheirids spent less time on the ground, their brachial enlargement and small sacral region indicating enhanced innervation of the wings and poor innervation of the sacrum and legs. This is the first study focusing on

pterosaur postcranial palaeoneurology; more studies on other taxa are needed to reveal patterns across Pterosauria as a whole.

Keywords: sacrum, palaeoneurology, computed tomography, pterosaur, foramina.

INTRODUCTION

Pterosaurs are a group of extinct flying archosaurian reptiles that inhabited the skies between the Late Triassic and the very end of the Cretaceous. The group encompasses substantial variation in size (wingspans range from c 50 cm to c 10 m) and marked diversity in feeding apparatus, proportions, wing form, and in inferred ecology and lifestyle (Witton 2013). Exceptional specimens that preserve integumentary soft tissues have provided substantial insight into pterosaur biology and anatomy (e.g. Unwin and Bakhurina 1994; Frey et al. 2003; Kellner et al. 2010), and phylogenetic hypotheses that find pterosaurs to be bracketed by crocodyliforms and lepidosaurs on one side and birds on the other (e.g. Sereno 1991; Hone and Benton 2007; Nesbitt 2011) allow us to make predictions about aspects of palaeobiology as yet not elucidated by the fossil record. Despite a recent burst of interest in pterosaurian anatomy and biology, several areas remain poorly understood and arguably understudied (especially in comparison to their close relatives, the dinosaurs); among these is palaeoneurology.

Historically, palaeoneurological studies have focused on the brains and endocasts of extinct vertebrates (e.g. archosaurs, Carabajal 2012; Sobral *et al.* 2016; Witmer *et al.* 2008; mammals, Macrini *et al.* 2007; amphibians, Romer and Edinger 1942; and fishes, Gai *et al.* 2011) and this is also true of pterosaurs. Pterosaur fossils are generally rare compared to other Mesozoic animals, and their skeletons were fragile, leaving their bones frequently crushed and distorted. Early studies of pterosaur endocasts focused on gross morphology visible in the broken or distorted fossils (e.g. Newton 1888; Bennett 2001), while more recent studies use X-ray computed tomography

(CT) imaging to reconstruct the morphology in complete, three-dimensionally preserved pterosaurs (Witmer *et al.* 2003; Codorniú *et al.* 2016).

Postcranial neurological studies in fossils, however, are even scarcer than those devoted to cranial structures and, among fossil archosaurs, have predominantly been restricted to crocodyliforms and dinosaurs. The presence of a lumbosacral enlargement – an area in the sacral vertebrae where the neural canal is enlarged compared to the rest of the spine, in some cases grossly enlarged – has long been recognised in dinosaurs, the structure variously being interpreted as some kind of "sacral brain" (e.g. Marsh 1881), or related to digestion or feeding (Branca 1914). However, Lull (1917) argued that this feature is common in many dinosaurs regardless of feeding strategy or size, and proposed a role related to innervation of the limbs. Studies on modern animals have noted an increase in spinal cord size in those regions to innervate the limbs in limbed animals, whereas limbless forms such as snakes lack cervical/brachial or lumbosacral enlargements (Kusuma *et al.* 1979). Similarly, Streeter (1904) noted that the brachial enlargement of ostriches was almost non-existent, whereas the lumbosacral enlargement was "enormous". One exquisitely preserved Eocene fossil salamander preserves soft tissue, including the lumbosacral plexus (Tissier *et al.* 2017).

Giffin (1990) introduced hypotheses formulated on these data to the field of palaeobiology; she described how correlations between the relative size of the spinal cord and increased innervation were linked to locomotory function and lifestyle in living animals, an idea then applied to a selection of fossil reptiles and mammals following examination of data on inferred nerve pattern and size. She found a close relationship between the size of the

neural canal and size of the spinal cord (Giffin 1995a; Giffin 1995b), though the relative size of the spinal cord compared to the neural canal does vary (Giffin 1990). She found that in *Alligator mississippiensis*, the cross-sectional area of the spinal cord is relatively constant throughout the vertebral column, occupying a maximum of 47% (in the brachial and lumbosacral maxima), and a minimum interlimb segment fill of 38%. While the pigeon (*Columba livia)* generally has a larger relative larger spinal cord (73% maximum vs. 53% minimum fill of interlimb segments), the overall pattern is the same. The lumbosacral regions of both the pigeon and the ostrich have spinal cord fills that are lower than the brachial and interlimb segments as well as in *Alligator* (29% and 32%, respectively; Giffin 1990). This is due to the presence of the glycogen body of birds, a structure not found in any other living vertebrates, or in the brachial region of birds. Although the fill percentage is lower in the lumbosacral region of birds, the overall cross-sectional area of both the spinal cord and the neural canal increases along with the spinal cord area in this region (Giffin 1990). This suggests that the size of the neural canal can be used as a proxy for the size of the spinal cord in a given section.

The size of the neural canal can be used to predict relative locomotory ability. The relative cord/canal size was studied first in extant lepidosaurs, birds, and crocodyliforms (Giffin 1990; Giffin 1995a; Giffin 1995b). For example, the sacral enlargement, which innervates the sacral plexus (lateral to the vertebral column on both sides) and therefore the hindlimbs, was relatively much larger relatively in an ostrich than in a pigeon or lizard, while the ostrich brachial enlargement (for innervation of the brachial plexus and therefore the forelimbs, also laterally to the vertebral column) was

comparatively small (Giffin 1990). She then applied this technique to non-avian dinosaur, crocodyliform, and plesiosaur fossils with semi-complete vertebral columns, with varying success. She was able to use neurological evidence to infer forelimb use in theropods via examination of data on their brachial enlargements: theropods with proportionally small forelimbs like *Tyrannosaurus* and *Carnotaurus* have comparatively smaller brachial enlargements than do *Deinonychus* and *Saurornitholestes* (Giffin 1995b). This method has also been successfully applied to modern and fossil marine carnivorans (Giffin 1992). Similarly, small brachial enlargement size in Haast's eagle (*Harpagornis moorei*) was used to suggest it lacked the neural development required for fine motor control, implying it could not have hunted in densely packed forests (Scofield and Ashwell 2009). More recently, O'Gorman and Fernandez (2017) drew from Giffin's work to infer the location of the brachial plexus in elasmosaurid plesiosaurs, important in determining regionalisation in the vertebral column of plesiosaurs.

Much of the work cited here was performed before the implementation of affordable, high resolution computed tomography (CT) imaging, and is thus of restricted use compared to modern data. Work prior to that of Giffin had certainly linked neural canal size with locomotion in – for example – non-avian dinosaurs (Lull 1917) and Triassic mammals (Jenkins and Parrington 1976), but Giffin's studies were the first to quantify the fossil data involved (Giffin 1990; 1992; 1995a; 1995b). The work relied on relatively complete vertebral columns that were free of matrix, or on published images (which do not always feature or reveal the necessary details). In our study, high resolution imaging by means of x-ray μ-CT scans provide data superior to that gleaned

both from direct observation of fossils and diagrammatic interpretations of them since an investigator can now examine the size of the neural structures in specimens that are still imbedded in matrix and where key features remain obscured to the human eye.

Our primary focus here is Pterodactyloidea, a diverse pterosaur clade characterised by reduction of the tail, elongation of the metacarpus, a proportionally large skull, and merging of the naris with the antorbital fenestra (Kellner 2003; Unwin 2003). Several lineages within this clade evolved substantially larger sizes than those present in non-pterodactyloid pterosaurs, though exactly how many times such size increases occurred is difficult to determine given that competing phylogenetic hypotheses for Pterodactyloidea differ substantially regarding the relationships between large-bodied taxa (Kellner 2003; Unwin 2003; Andres and Myers 2013; Vidovic and Martill 2017). Several aspects of wing specialisation, combined with hindlimb reduction, increased skeletal pneumatisation and other features indicate that, when compared to non-pterodactyloids, pterodactyloids of many species were highly aerial, and proficient flight abilities were clearly typical of species across the group (e.g. Bramwell and Whitfield 1974; Wilkinson 2008; Palmer 2011). However, limb and pelvic anatomy, augmented by copious data from trackways (e.g. Hwang et al. 2002; Lockley and Rainforth 2002; Mazin et al. 2009), demonstrates that many of these animals were also adept terrestrial locomotors, and that members of some groups may even have foraged and fed extensively on the ground (Witton and Naish 2008, 2015; Naish and Witton 2017). Members of Azhdarchoidea in particular – the toothless, Cretaceous clade that includes the typically gigantic, long-jawed azhdarchids,

the short-faced tapejarids, and the intermediate chaoyangopterids and thalassodromids – appear well adapted for terrestrial behaviour; in particular the azhdarchids with their long hindlimbs and compact feet (Witton and Naish 2008, 2015; Witton 2013). Conversely, other pterodactyloids – ornithocheirids (*sensu* Unwin 2003) among them – are thought to have been less terrestrially capable, and to have been specialised for the capture and consumption of prey while flying (Witton 2013).

Vectidraco daisymorrisae is an azhdarchoid pterodactyloid pterosaur from the Aptian aged Atherfield Clay Formation of the Isle of Wight, UK, described from an articulated pelvis, sacrum, and partial vertebral column with a preserved pelvic length of just 40 mm (Naish *et al.* 2013). The vertebrae were originally described as one dorsal and three sacrals, and possessing large, paired pneumatic foramina located dorsolaterally on the centra. As noted by Naish et al. (2013) and Hyder et al. (2014), the pterosaur pelvis has received little attention compared to the rest of the body and numerous questions relating to anatomy, function and variation in this part of skeleton have yet to receive investigation.

To investigate the potential significance of the small overall size and proportionally large pneumatic foramina of this specimen, we studied its anatomy using 3D µ-CT scan data. Unexpectedly, interesting data was also obtained for the neural canal and gross neuroanatomy of the vertebral column which we then compared to CT scan data obtained from two other pterosaurs: the ornithocheirids *Anhanguera* and *Coloborhynchus robustus*. In contrast to *V. daisymorrisae*, both *Anhanguera* and *C. robustus* have relatively complete vertebral columns.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; NHMUK, Natural History Museum, London, UK; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany.

MATERIALS AND METHODS

NHMUK PV R36621 is the holotype and only specimen of *Vectidraco daisymorrisae*, represented by a partial pelvis and articulated sacral and dorsal vertebra (Fig. 1A; Naish*, et al.* 2013). Micro-CT scans of the specimen were taken at the Natural History Museum using a Nikon Metrology HMX ST 225 scanner, at 210 kV and 190 µA with a 1 mm copper filter, to a voxel size of 35 µm. CT scans of the sacrum and pelvis of AMNH FARB 22555 (Fig. 1B), a partially complete skeleton of *Anhanguera santanae,* were made at Stony Brook University Hospital in 2003 and provided by P. O'Connor. Details are available in Claessens et al. (2009). AMNH FARB 22555 is typically referred to in the literature as *Anhanguera santanae* (e.g. Wellnhofer 1991; Claessens et al. 2009), although a recent study suggests there is not enough information to refer it to this species (Pinheiro and Rodrigues 2017): we therefore refer to it as *Anhanguera* here. SMNK PAL 1133, a partially complete *Coloborhynchus robustus* with a complete articulated sacrum (Fig. 1C; Elgin 2014), was CT scanned at the µ-VIS X-Ray Imaging Centre at the University of Southampton, using a custom built 450 kVp/225 kVp walk-in CT scanner. The scans were conducted using the 450 kVp source at 250 kVp and 482 µA to a voxel size of 132 µm.

The anatomy of each specimen was then studied and analysed using the Fiji/ImageJ (Schindelin *et al.* 2012) and Avizo 8.1 (FEI Visualization

Sciences Group, France) software packages. Dimensional data on neural canal size was collected at the junction of each vertebra in the sacrum, or at the anterior-most point that is preserved (note that the collection of this data is not contingent on CT-scan images, as long as individual vertebrae are disarticulated when preserved or prepared). Neural canal area and centrum face area were calculated by shading the area of each portion followed by the "Analyze particles" option in Fiji. These were then compared directly and, via the use of ratios (neural canal area to centrum area), were normalised for size to ease comparison.

Centrum face area was used as a comparative measurement for neural canal area as it was a standard measurement that could be taken on each vertebra in all specimens. A standard, easily measured feature was required for each specimen, and we feel this was the best feature to normalise for size and compare between specimens. We recognise that the size of the centrum may vary based on other features such as size of the animal or biomechanical constraints. However, because it is normalised to a ratio in order to eliminate the possibility of size affecting our conclusions, and since we are comparing between relatively closely-related pterosaur taxa, we feel that this method is a reasonable compromise given the paucity of data available. Additionally, we assume that pterosaurs are relatively conservative in centrum morphology. There are no current indications that pterosaur taxa were so significantly different in their morphology (and therefore in any biomechanical forces in the vertebral column) that the use of centrum size would be particularly inaccurate. While the number of vertebrae in a pterosaur sacrum or synsacrum and the shape of the neural arch including a presence/absence of

a supraneural plate may vary (e.g. Bennett 1990; Bennett 2001; Witton 2013), general morphology does not. For this reason, using the centrum area for normalisation to compare between an azhdarchoid (*Vectidraco daisymorrisae*) and two ornithocheiroids (*Coloborhynchus robustus* and *Anhanguera*) likely will not introduce significant errors. Further studies on the variation of centrum size, especially between different taxa, are needed to further understand this problem better.

DESCRIPTION AND RESULTS

Vectidraco *lateral foramina*

To discuss the lateral foramina, we must first provide an updated anatomical interpretation of *Vectidraco daisymorrisae* in view of new data on the correct number of vertebrae present. The original description identified four vertebrae: one dorsal, and three sacrals (Naish*, et al.* 2013). The vertebrae were stated to possess “ventral bulges” on the centrum, the implication being that these were not homologous with the fused and expanded junctions seen at the junctions of the fused sacral vertebrae. However, CT data indicates that these bulges are indeed the fused junctions of vertebrae within the sacrum. We therefore suggest the presence of six vertebrae: the posterior-most dorsal vertebra (which is fused to the first true sacral, creating a synsacrum like that seen in *Pteranodon*; Bennett 2001), and five sacrals (Fig. 2). Four sacral ribs are present, and evidence for a fifth can be seen on the lateral side of the first sacral vertebra and medial side of the ilium (Fig. 1A). The neural spine of the first sacral is not preserved.

The CT scans of the *V. daisymorrisae* sacrum show that the foramina previously identified as large, paired lateral pneumatic foramina communicate with the neural canal, decreasing in cross-section medially as they reach the neural canal (Fig. 2). These foramina do not enter and excavate either the centra or the neural spines of any vertebrae in *Vectidraco* suggesting that they are not pneumatic: instead, we conclude that they are the openings for passage of the spinal nerves as they exit the spinal cord and neural canal between adjacent vertebrae, an interpretation consistent with our reinterpretation of vertebral number and relationships given previously. These openings are commonly referred to as intervertebral foramina. Although the location of these foramina in *V. daisymorrisae* do not always appear exactly at the junction between two vertebrae, CT scans indicate that intervertebral foramina often appear externally as if they were anterior to the junction but are directed posteriorly, meeting the neural canal at the junction. Pneumatic foramina are still present in *V. daisymorrisae*, specifically on the dorsolateral side of the zygapophyses of the sacral vertebra; pneumatic excavations are also present on the neural spines and neural arches (Fig. 3). The intervertebral foramina of *V. daisymorrisae* are much larger in size externally than the pneumatic foramina (1.76-2.04 mm vs. 0.39 mm; Table 1).

Intervertebral foramina are also present in the sacra of both *Coloborhynchus robustus* (SMNK PAL 1133) and *Anhanguera santanae* (AMNH FARB 22555) (Fig. 4). In both cases, these can be observed with and without CT scanning.

Neural canal patterns

Coloborhynchus and *Anhanguera* do not exhibit the enlarged sacral neural canal usually representative of the presence of a lumbosacral enlargement in other diapsids (Giffin 1990, 1995b; Giffin 1995a; O'Gorman and Fernandez 2016; Table 2, Figs 5, 6). In contrast, *Vectidraco daisymorrisae* has the smallest sacrum of the three pterosaurs studied (and is presumably the smallest animal), yet possesses what is clearly the largest sacral neural canal in comparision to its size. By direct comparison of absolute values, the sacral neural canal in *Vectidraco* is similar in size to that of *Anhanguera*, but smaller than that of *Coloborhynchus* (Fig. 5A). When normalised for size (via the use of a ratio comparing neural canal size with the size of the articular face of the centrum), *Vectidraco* and *Coloborhynchus* have similarly sized sacral neural canals, while *Anhanguera*'s is much smaller (Fig. 4B).

Elsewhere in the vertebral column, both *Anhanguera* and *Coloborhynchus* possess a brachial enlargement at the notarium, presumably for innervation of the brachial plexus (Fig. 6). In both cases, the brachial enlargement is larger than the sacral neural canal in the same animal. The brachial enlargement is larger in *Coloborhynchus* than it is in *Anhanguera*, especially in direct comparison, and to a lesser extent in normalised comparison (Fig. 6). Because *Vectidraco* is known only from a partial sacrum, it is currently unknown whether it possessed an enlarged brachial enlargement or not.

DISCUSSION

Intervertebral foramina and pneumatic foramina in pterosaur sacra

The identification of intervertebral foramina in the sacrum of *Vectidraco* is unsurprising given that such structures were likely ubiquitous across archosaurs and vertebrates (Walker 1988); despite this, they have gone virtually undiscussed in the literature. This might, in part, be due to the frequent poor preservation of pterosaur pelves and sacra, but it is more likely the consequence of under-study and general lack of interest in the pterosaurian pelvis, combined with their previous confusion with pneumatic structures.

Naish et al. (2013) created a phylogenetic analysis based on pelvic characters and noted how previous authors had variously used 0, 1 or 2 characters from the pelvis in supposedly representative scoring of the pterosaur skeleton. Our study also indicates the effectiveness of using CT imaging to determine anatomical characters. While some pterosaur sacra can be prepared in such a way that the intervertebral foramina are clearly visible (e.g. SMNK PAL 1133 and AMNH FARB 22555), others are too fragile or small to remove the matrix: *Vectidraco* itself being one such example, this leading to the incorrect identification of the intervertebral foramina as pneumatic foramina. Given that the only unambiguous evidence of postcranial skeletal pneumaticity in fossils is the presence of a large internal chamber opening externally via a foramen (Britt 1993; O'Connor 2006; Wedel 2007), CT is often the only non-destructive way to determine if either; a) large internal chambers are present; or b) the foramen connects both the external of the bone and the internal chamber. For this reason, CT scans are increasingly being used to determine the pneumatic nature of fossil bones (e.g. Claessens *et al.* 2009; Wedel 2008; Martin and Palmer 2014a;

Watanabe *et al.* 2015). As such, we strongly recommend the use of CT to aid in determining the pneumatic nature of fossil bones, especially when they are embedded in matrix. However, it does appear that intervertebral foramina are significantly larger than pneumatic foramina (Table 1), and that size combined with location may be an indicator of foramina identification in pterosaurs, in the absence of CT scans.

Implications for palaeoecology

Enlarged sections of the diapsid spinal cord in the brachial and lumbosacral regions help to innervate the brachial and lumbosacral nerve plexuses (Kusuma*, et al.* 1979). It is from these regions that the large nerves responsible for innervating the limbs exit the spinal cord, unite to form the plexuses, and then continue distally along the limbs. Both *Anhanguera* and *Coloborhynchus* show no obvious lumbosacral enlargements, and *Vectidraco* does not preserve a sufficiently complete vertebral column to say whether or not it was enlarged. However, pterosaurs presumably still possessed a lumbosacral plexus consistent with that present in other diapsids and required for innervation of the hindlimb. The relatively large lumbosacral region of the spinal cord (assumed from the relative size of the sacral neural canal) of *V. daisymorrisae* is interesting, especially when compared to *Anhanguera* and, to a lesser extent, *Coloborhynchus* (see below for details). The large lumbosacral cord suggests that the hindlimbs of *Vectidraco* were relatively highly innervated compared to those of *Anhanguera*, but potentially innervated in a manner similar to those of *Coloborhynchus*. Based on the limb-level nerve/vertebral relationships reported by Giffin (1995a) to be

present in lizards (Mivart and Clarke 1877), crocodylians (Bronn 1890) and birds (Boas 1933), this increased innervation likely involved the sciatic nerve, and possibly the femoral and obturator nerves as well.

In several diapsid groups, both overall spinal cord size overall and the size of spinal enlargements have been shown to relate closely to locomotion and limb function. Kusuma et al. (1979) found that limbless lizards or snakes have no cervical/brachial or lumbosacral enlargements at all, since there are no limbs to innervate and therefore no need for large innervation in these regions. However, crocodylians, turtles and other reptiles all showed obvious enlargements of the spinal cord related to the development and location of their limbs, and those with well-developed posterior extremities possessed especially large lumbosacral enlargements. Ostriches – the wings of which are not used in locomotion but only in relatively simple movements relevant to display and balance – have a small brachial enlargement and a far larger lumbosacral enlargement (Streeter 1904; Giffin 1995b). Additionally, for a given body size, the brachial enlargement appears to be smaller in non-flyers than it is in weak flyers, while weak flyers in turn generally have smaller brachial enlargements than strong flyers, although there are exceptions to this (Giffin 1995b). Finally, typical birds (e.g., the pigeon *Columba*) that rely on both their legs for walking and takeoff and their wings for flying have similarly sized brachial and lumbosacral enlargements (Giffin 1995b). Relative spinal cord enlargement size appears to be somewhat related to at least relative locomotory performance, a generalisation that can be applied tentatively here. A caveat is that none of Giffin's studies used any kind of phylogenetic control and were not put into any phylogenetic context. Given that species are not

independent in terms of statistical analyses and correlations between variables (e.g. Freckleton et al. 2002), it is important to take this into account where possible.

Vectidraco was hypothesised by Naish *et al.* (2013) to be a small-bodied member of Azhdarchoidea, their phylogenetic analysis hinting at a position outside of Neoazhdarchia and close to tapejarids. This interpretation is important with respect to data on the size of the lumbosacral spinal cord and the information this potentially provides on the unknown hindlimbs of *Vectidraco*. Azhdarchoidea (*sensu* Unwin 2003 and Kellner 2003) – a clade currently understood to contain Tapejaridae, Chaoyangopteridae, Thalassodromidae and Azhdarchidae – is thought to be one of the most terrestrially adept pterosaur groups. Azhdarchoid fossils tend to be found in continental or marginal marine deposits (Witton and Naish 2008, 2015; Witton 2013), a hypothesis consistent with isotopic data suggesting terrestrial occurrence and association with freshwater (Tütken and Hone 2010). Morphological evidence – including long, slender legs and the configuration of the pelvis – strongly supports competent terrestrial abilities in azhdarchids (Witton and Naish 2008; Hyder *et al.* 2014); a purported azhdarchid trackway from the Upper Cretaceous of Korea also indicates efficient terrestrial locomotion in this group (Hwang *et al.* 2002; Witton and Naish 2008).

Particularly important is the large postacetabular process of Neoazhdarchia, thought to anchor large hindlimb musculature (Hyder *et al.* 2014). Both the postacetabular process, thought to anchor *m. iliofibularis* (Frigot 2017), and the larger lumbosacral spinal cord of *Vectidraco* strongly support the hypothesis that this animal was terrestrially adept, and more so

than larger, non-azhdarchoid pterosaurs like *Anhanguera*. Without the rest of the vertebral column for *Vectidraco*, we cannot comment on its relative aerial capabilities or whether or not it has a lumbosacral enlargement, only that it appears to have more highly innervated hindlimbs than at least some ornithocheirids (e.g. *Anhanguera*), a fact consistent with a more terrestrial lifestyle. Of incidental note here is that Dsungaripteridae is included within (Andres and Myers 2013), or as sister-group (Kellner 2003; Unwin 2003) to Azhdarchoidea, and also provides clear evidence for terrestrial proficiency, namely the thick-walled, curved femora (Fastnacht 2005), relatively long hindlimbs, and presence in terrestrial sediments (Witton 2013). However, more information is needed to investigate the biomechanics and palaeobiology of this group further.

However, the argument for poor terrestrial capabilities in ornithocheirids vs. strong capabilities in azhdarchoids potentially breaks down with respect to *Coloborhynchus*, as both *Vectidraco* and *Coloborhynchus* have similarly sized lumbosacral spinal cords (Table 2, Figs 5, 6). The Romualdo Formation of Brazil, where both *Anhanguera* (AMNH FARB 22555) and *Coloborhynchus* (SMNK PAL 1133) were found, has yielded as many as seven valid ornithocheirid genera according to some authors (e.g. *Anhanguera*, *Barbosania*, *Brasileodactylus*, *Cearadactylus*, *Coloborhynchus*, *Santanadactylus*, and *Ornithocheirus*; Elgin and Frey 2011). This interpretation may suggest that many morphologically similar species were occupying similar niches. If – we speculate – some ornithocheirids, such as *Coloborhynchus,* were more adept on land, this could allow the occupation of a marginally different niche, thereby preventing the competition we otherwise

see as potentially problematic. More taxa and specimens of these genera and species are needed to address this question further, as well as further anatomical studies on the hindlimbs and pelvis of *Coloborhynchus.*

The large brachial enlargement reported here for ornithocheirids is also noteworthy from a palaeoecological context. Both *Coloborhynchus* and *Anhanguera* show larger brachial enlargements than lumbosacral enlargements, and indeed they seemingly do not show any lumbosacral enlargement at all (Table 2, Fig. 6). This increased brachial enlargement size indicates a considerable brachial plexus for the ulnar, radial, and median nerve roots for innervation of the forelimbs/wings (see the nerve structures in a lizard, Lecuru-Renous 1968; crocodylian, Bronn 1890; and bird, Bubien-Waluszewska 1985, as seen in Giffin 1995b). This configuration is the opposite of that present in ostriches (Streeter 1904; Giffin 1995b), and differs from the generally similarly-sized enlargements seen in other birds (Giffin 1995b). On the basis of this bird-led data, we interpret the size disparity (Table 2, Fig. 6) between the brachial enlargement and lumbosacral spinal cord in the ornithocheirids *Coloborhynchus* and *Anhanguera* to indicate a substantially heavier reliance on the forelimbs in these pterosaurs. This agrees with other lines of evidence showing that ornithocheirids were more aerially than terrestrially adapted (see Witton 2013 for summary). However, this does not negate the evidence mentioned previously that *Coloborhynchus* may have been more terrestrially adapted than *Anhanguera* – they both may have been relatively poor terrestrial locomotor, but with differing degrees of terrestriality between them. Additionally, analysis of their pelvic musculature and relatively short hindlimbs imply that they would have been poor terrestrial

locomotors (Witton 2013; Hyder*, et al.* 2014). This is important when discussing the possible launch mechanism of pterosaurs.

While many studies have assumed that pterosaurs took off in a similar matter to birds – relying on their hindlimbs to launch themselves into the air using a jump or running takeoff (e.g. Bramwell and Whitfield 1974; Chatterjee and Templin 2004; Sato *et al.* 2009) – more recent analyses have suggested that larger pterosaurs were significantly heavier than previously thought, and that they may have taken off using a quadrupedal launch similar to that of some bats (e.g. Habib 2008; Witton 2008; Henderson 2010; Martin and Palmer 2014b). Use of a quadrupedal launch would decrease reliance on the hindlimbs and pelvis during takeoff, rendering them significantly less important, in functional terms, than those of birds. It follows that less reliance on the pelvis during interaction with the substrate would not require a large lumbosacral spinal cord and plexus as this would add additional mass that would be a hindrance during flight. It should be mentioned that the presence of a brachial enlargement that is larger than the lumbosacral one reported in *Crocodylus* by Giffin (1995b) was attributed to frontal accumulation resulting from an increased number of ascending and descending nerve fibres approaching the cranium, rather than to increased innervation of the limbs as discussed here for pterosaurs. However, seeing as the pterosaurs included in our study do not possess gradual posterior decrease in the size of the neural canal of the non-enlarged dorsal vertebrae (at least not in those vertebrae present), we feel that a link with innervation rather than frontal accumulation better serves as an explanation.

The increased size of the pterosaurian brachial enlargement is likely due to both the relatively large size of their forelimbs and high density of innervation: features that are not related exclusively to size, but also to the requirement for pterosaur wings to be highly maneuverable and for the significant, near-constant manipulation of the flight membrane required during flight. Our logic here is consistent with Scofield and Ashwell's (2009) observation that the small size of the brachial enlargement in Haast's eagle relates to its poor fine motor skills rather than low-powered wing muscles. There is currently no clear way to determine whether pterosaur wings had an increased density of innervation. However, it seems reasonable to assume that both the substantial quantity of musculature associated with the powerful wings and the potential need for fine motor control of the flight surfaces would support the need for high innervation in this region.

Effects of ontogeny and size

It is important to discuss the potential impact of ontogeny and size on the form of the spinal cord and its enlargements, especially with respect to *Vectidraco*: *Vectidraco* is significantly smaller than the other pterosaurs studied here, its estimated wingspan being less than 1m (Naish*, et al.* 2013). Is the relatively large size of the lumbosacral enlargement in this taxon a consequence of a potential juvenile status? Two lines of evidence dispute this. Firstly, the only known *Vectidraco* specimen appears to be a small-bodied adult, there being no evidence to suggest that it was a juvenile. Naish *et al.* (2013) list a number of features that indicate osteological maturity in this individual, including closed sutures between pelvic bones, fusion of neural

arches to centra, fully ossified pelvic bones, and fusion of the sacral ribs to the sacrum. We found no indications that these observations were incorrect, including no presence of the pitted or grainy bone texture typical of in juvenile pterosaurs (Bennett 1993). Secondly, osteologically juvenile pterosaurs (vernacularly termed ‘flaplings’ by Unwin 2005) appear to be well adapted for flight; even embryos possess well-developed wings (e.g. Wang and Zhou 2004; Chiappe *et al.* 2004; Witton *et al.* 2017) indicating that they were likely flight-capable soon after hatching (Unwin 2005; though see Wang *et al.* 2017 for an alternative view). Ergo, there is no reason to believe that the lumbosacral enlargement – or any structure related to terrestrial locomotion – would be any larger in a juvenile than an adult. Furthermore, the *Anhanguera* specimen AMNH FARB 22555 appears to have a smaller lumbosacral enlargement than *Vectidraco* with respect to its size, and it is not mature; the lack of co-ossification of such elements such as the carpals and scapulacoracoid indicate subadult status (Wellnhofer 1991).

With ontogeny disregarded, could the overall size of *Vectidraco* provide an alternative explanation for its large lumbosacral enlargement? Hallgrímsson and Maiorana (2000) found that smaller mammals and birds have significantly lower mass variability across species because a specific amount of mass must be devoted to organs and systems, a fact especially relevant to the nervous system and brain. Essentially, there is a minimum amount of nervous tissue that is required to sufficiently innervate a vertebrate due to functional constraints, and this appears to compose a smaller percentage of the entire body mass in larger animals, as it does not scale in a positively allometric fashion (Hallgrímsson and Maiorana 2000). However,

other tissues such as fat and muscle vary more based on environmental factors, thus forming significantly larger portions of total body mass. The brain makes up a larger percentage of total mass in smaller animals than larger ones, and a similar relationship presumably also extends to the central and peripheral nervous systems (Hallgrímsson and Maiorana 2000). This might partially explain the large lumbosacral spinal cord of *Vectidraco* given that the animal is so much smaller than both *Anhanguera* and *Coloborhynchus*. However, if the proportional size of the spinal cord with respect to total body size was the only control influencing relative size of the spinal cord in the sacral region, we would not expect that of *Vectidraco* to be the same exact size as it is significantly larger pterosaurs, and the latter is the observed condition.

CONCLUSION AND FUTURE STUDIES

To summarise, *Vectidraco daisymorrisae* has an unusually large sacral neural canal, and is therefore inferred to have had a significantly large lumbosacral spinal cord, and likely lumbosacral plexus, with respect to *Anhanguera*. We take this as evidence that it may have been a proficient terrestrial locomotor, a hypothesis consistent with data from azhdarchoids in general (Witton & Naish 2008, 2015; Witton 2013). In contrast, the larger brachial enlargement (with respect to the lumbosacral enlargement) seen in ornithocheirids is consistent with data indicating that these animals spent little time on land and were highly aerial, perhaps being on par with extant frigatebirds (Palmer 2011). Such forelimb-dominance is consistent with substantial innervation of the wings. This adds support to the quadrupedal

launch hypothesis as poorly innervated hindlimbs would be insufficient on their own for takeoff in the manner typical for birds. However, it should be noticed that as there is no preserved notarium, or anything other than a sacrum in *Vectidraco*, it is unclear how large the brachial spinal cord would be, nor do we understand the relative size of the brachial enlargement relative to the lumbosacral one.

Our study should be seen as an initial foray into the study of postcranial palaeoneurology in pterosaurs, and significantly work remains to be done in this field. The small sample size here should be expanded, and our palaeoecological inferences are tentative without additional data, especially without a set of complete vertebral columns for comparison. Future work should look at additional sacra to see if the patterns reported here are consistent across pterosaurs, and look for variation across ontogeny and the size spectrum present within this clade; data from complete vertebral columns should also be obtained. Further studies should also look at the variation of neural canal size and vertebral centrum size within a phylogenetic context, taking into account the relatedness of the species in question (something not possible with a sample size of three). Additionally, it would be beneficial to conduct further validation studies on modern taxa, especially in a wide selection of birds of differing flight habits, and potentially in bats, in order to improve our knowledge of groups comparable to pterosaurs. While the pelvis has not been as well studied as have other parts of pterosaur anatomy (Naish *et al*. 2013), recent studies on pelvic evolution (Hyder*, et al.* 2014) and musculature (Frigot 2017; Costa *et al.* 2014) have at least provided a

foundation for our understanding of pterosaur pelvic anatomy and biomechanics.

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DATA ARCHIVING STATEMENT

CT scan data from this study are available in Dryad (SMNK PAL 1133 *Coloborhynchus robustus*; https://doi.org/10.5061/dryad.rq4b2n6), and MorphoSource (NHMUK PV R36621 *Vectidraco daisymorrisae*, and AMNH FARB 22555 *Anhanguera santanae*; access using username: reviewers@reviews.com, pwd: 12345678). [These files will be made public

upon acceptance of the paper, at which time an updated link for the MorphoSource data will be provided]

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Figure captions

Figure 1: Three pterosaur specimens used in this study in dorsal (top) and left lateral (bottom) views. A) *Vectidraco daisymorrisae* (NHMUK PV R36621) partial sacrum and pelvis, dorsal view photo by Barry Marsh; B) *Anhanguera* (AMNH FARB 22555) dorsal vertebrae, sacrum, and pelvic block; C) *Coloborhynchus robustus* (SMNK PAL 1133) sacrum. Scale = 50 mm.

Figure 2: *Vectidraco daisymorrisae* (NHMUK PV R36621) sacral vertebrae in right lateral view with CT slices (transverse plane) showing intervertebral foramina. Dashed lines indicate approximately where each CT scan was taken, yellow arrows indicate right intervertebral foramina, anterior is to the right. ce, centrum; DV, dorsal vertebra; nc, neural canal; ns, neural spine; S = sacral vertebra with corresponding number. Images not to scale.

Figure 3: CT scan of the posterior-most dorsal vertebra of *Vectidraco daisymorrisae*. Yellow arrows indicate pneumatic foramina, white arrows show pneumatic excavations not connected to the exterior in this slice.

Figure 4: Sacra in left lateral view of two pterosaurs with CT images showing intervertebral foramina. A) *Anhanguera* (AMNH FARB 22555) fused posterior pelvic/sacral block; B) *Coloborhynchus robustus* (SMNK PAL 1133) fused sacrum. Dashed lines indicate approximately where each CT scan was taken, yellow arrows indicate left intervertebral foramina, anterior is to the left. Ce, centrum; nc, neural canal. Images not to scale.

Figure 5: Neural canal area comparisons in three pterosaur sacra. A) Centrum area vs. neural canal area in three pterosaur sacra, with linear regression lines: *Vectidraco daisymorrisae*, y = 0.538x – 1.738 (R^2 = 0.835); *Coloborhynchus robustus*, y = 0.276x + 11.182 (R^2 = 0.900); *Anhanguera*, y = 0.215x – 4.413 (R^2 = 0.888). B) Normalised neural canal area (ratio of centrum area to neural canal area as seen in A at different vertebral junctions in the sacrum identified at the anterior articulation of the vertebra number listed. Sacral vertebrae are represented by segments 23 to 27, as seen in *Vectidraco daisymorrisae*.

Figure 6: Neural canal area comparisons across the entire vertebral column of three pterosaurs. A) Neural canal area measured at the anterior junction of different vertebrae; B) Normalised neural canal area (ratio of centrum area to neural canal area as seen in A) at different vertebral junctions identified at the anterior articulation of the vertebra number listed. Notarium represented between cervical vertebra 9 (position 9) and dorsal vertebra 5 (position 14). Sacral vertebrae are represented by segments 23 to 27, as seen in *Vectidraco daisymorrisae*. Gaps represent vertebrae that are not present, or areas that were not measureable. **be** indicates approximate location of the brachial enlargement, **lse** indicates approximate location of the lumbosacral “enlargement”. Vertebral segment numbers derived from AMNH FARB 22555 and Wellnhofer (1991).

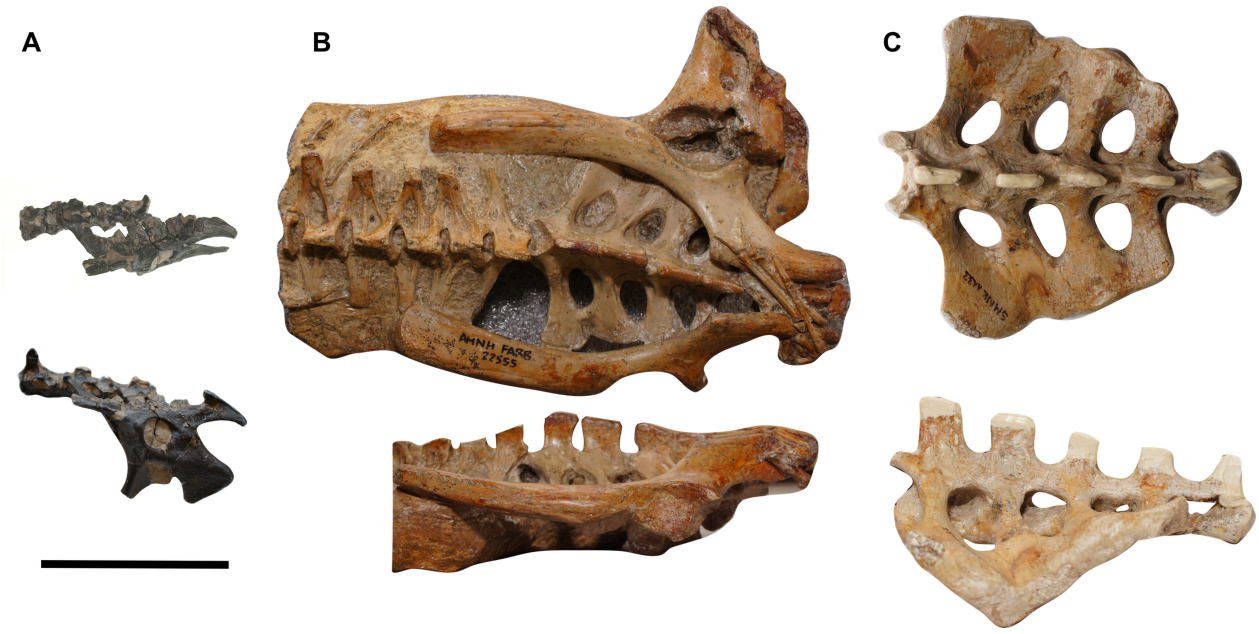
Tables

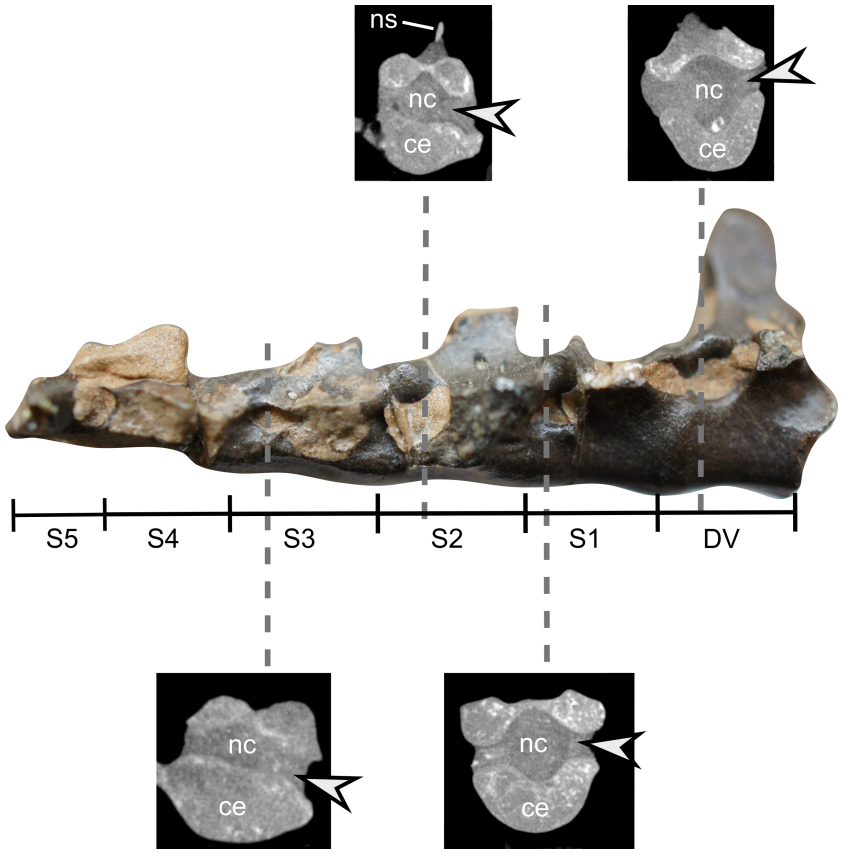
Location	Max. foramen width (mm)
DV, ivf	2.04
S1, ivf	1.91
S2, ivf	2.92
S2, pf	0.39
S3, ivf	1.76

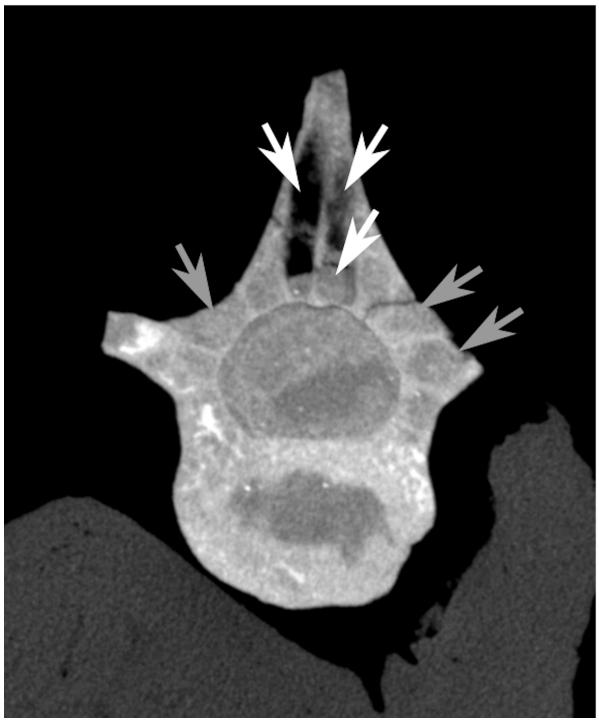
Table 1: Exterior measurements from selected foramina on the right side of *Vectidraco daisymorrisae* (NHMUK PV R36621). Measurements were taken of the maximum width of the foramina from the exterior surface, in a roughly antero-posterior direction. DV, dorsal vertebra; S, sacral vertebra; ivf, intervertebral foramina; pf, pneumatic foramina.

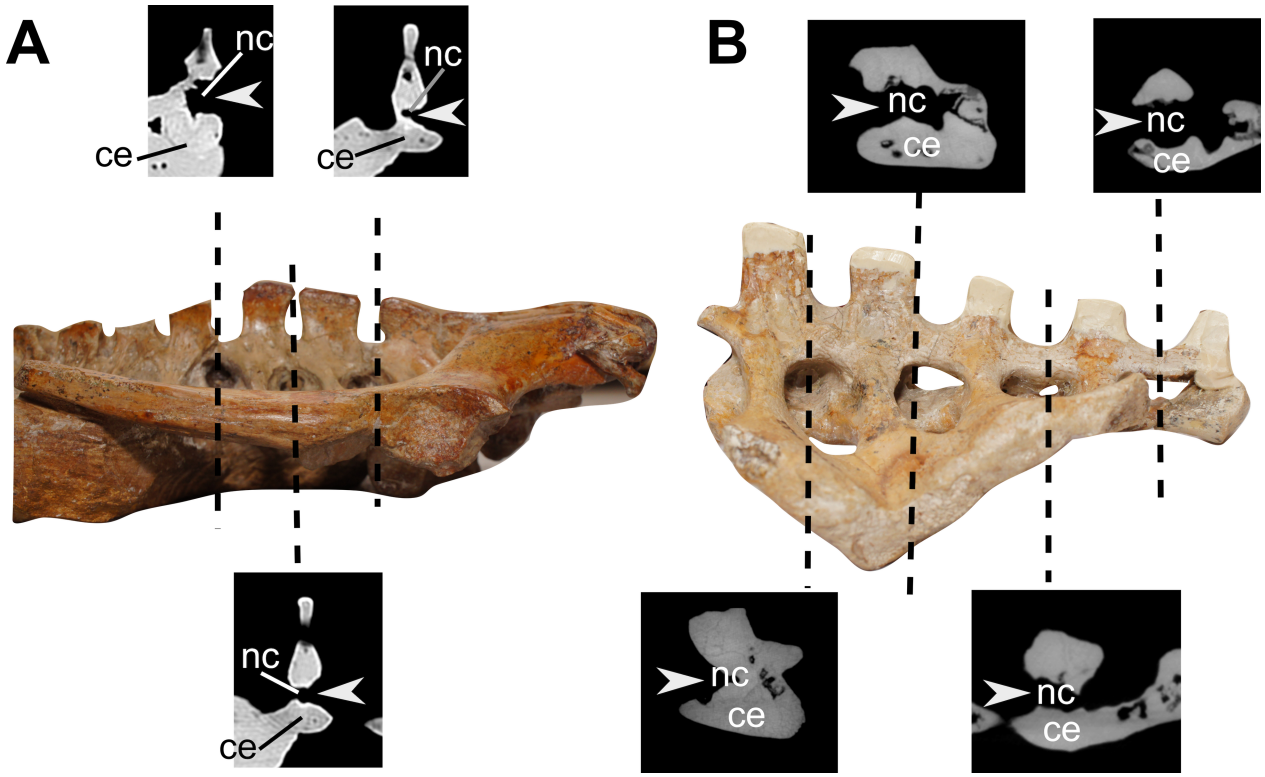
Vertebral Segment	*Vectidraco* NHMUK PV R36621			*Coloborhynchus robustus* SMNK PAL 1133			*Anhanguera* AMNH FARB 22555		
	nc area	c area	ratio	nc area	c area	ratio	nc area	c area	ratio
1									
2									
3				67.09	145.97	0.46			
4									
5									
6				19.66	186.26	0.11	16.91	181.69	0.09
7				49.56	129.81	0.38			
8									
9 (N)				74.68	244.73	0.31	40.50	84.48	0.48
10 (N)				131.99	370.87	0.36	19.06	80.30	0.24
11 (N)				112.45	342.09	0.33	17.75	59.24	0.30
12 (N)				119.84	243.45	0.49	21.38	70.49	0.30
13 (N)				118.78	195.92	0.61	23.52	65.46	0.36
14 (N)				74.35	150.44	0.49	26.09	63.49	0.41
15 (N)							9.91	68.41	0.14
16							15.36	65.64	0.23
17									
18				69.70	122.81	0.57			
19				64.43	161.50	0.40			
20				80.83	178.96	0.45			
21									
22							11.39	63.74	0.18
23 (S)	9.56	18.14	0.53				13.32	86.63	0.15
24 (S)	8.13	19.65	0.41	64.79	196.58	0.33	6.22	45.46	0.14
25 (S)	7.80	16.76	0.47	137.67	137.67	0.39	3.90	47.46	0.08
26 (S)	3.08	12.76	0.24	28.10	85.38	0.33	2.81	34.45	0.08
27 (S)	1.71	5.09	0.34	18.33	44.84	0.41			
28 (S)				28.76	35.52	0.81			

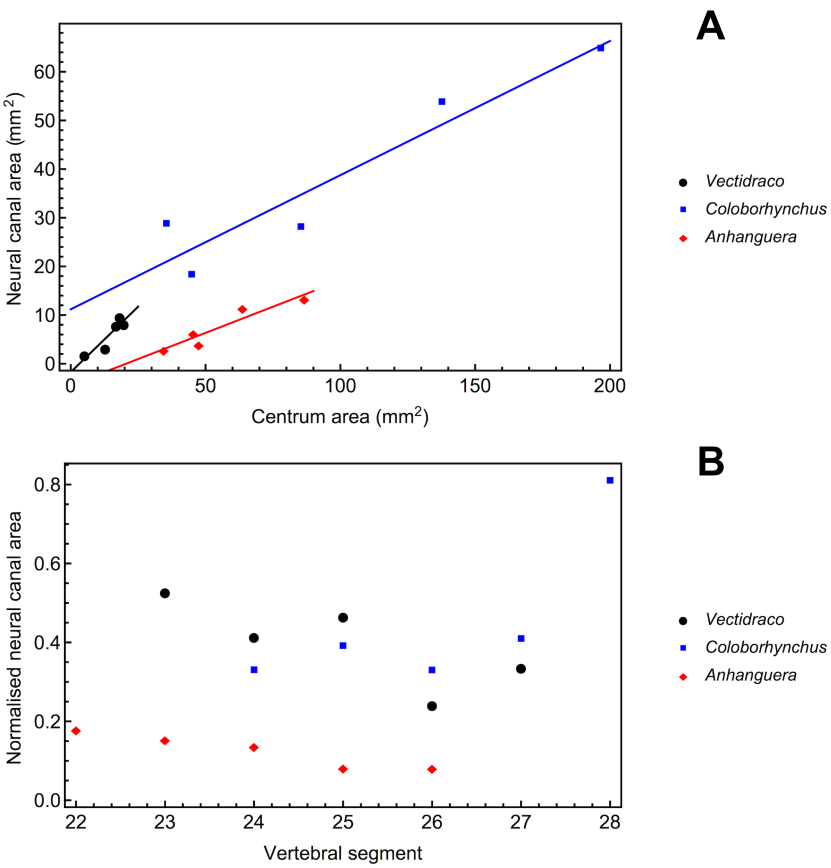
Table 2: Neural canal and centrum area (mm^2) taken from the neural canal of three different pterosaur specimens, throughout the vertebral column at different vertebral segments, and the normalised ratio of neural canal to centrum area. nc = neural canal; c = centrum; N indicates segments making up the notarium; S indicates segments making up the sacrum.

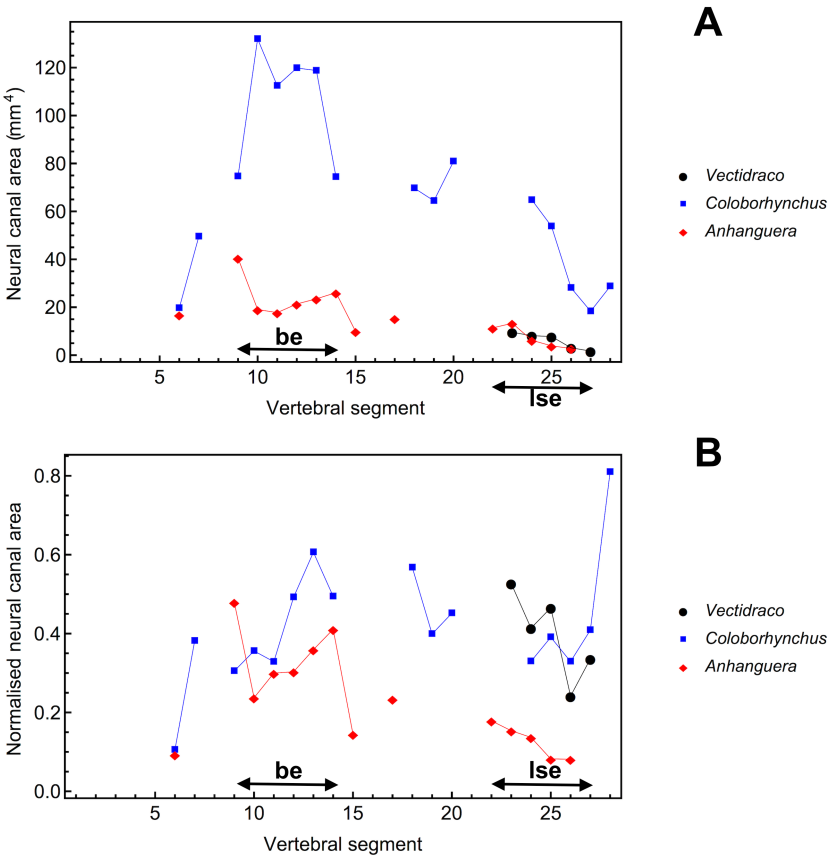

A
B
C
AMNH FARB
27355


ns
nc
ce
nc
ce
S5
S4
S3
S2
S1
DV
nc
ce
nc
ce




A
nc
ce
nc
ce
nc
ce
B
nc
ce
nc
ce
nc
ce
nc
ce


A
Neural canal area (mm2)
Centrum area (mm2)
0
10
20
30
40
50
60
0
50
100
150
200
Vectidraco
Coloborhynchus
Anhanguera
B
Normalised neural canal area
Vertebral segment
0.0
0.2
0.4
0.6
0.8
22
23
24
25
26
27
28
Vectidraco
Coloborhynchus
Anhanguera


A
Neural canal area (mm4)
120
100
80
60
40
20
0
5
10
15
20
25
Vertebral segment
be
lse
Vectidraco
Coloborhynchus
Anhanguera
B
Normalised neural canal area
0.8
0.6
0.4
0.2
0.0
5
10
15
20
25
Vertebral segment
be
lse
Vectidraco
Coloborhynchus
Anhanguera